High primary production and vertical export of carbon over the Kerguelen Plateau as a consequence of natural iron fertilization in a high-nutrient, low-chlorophyll environment

by

Bernard QUÉGUINER* (1), Stéphane BLAIN (2) & Thomas TRULL (3)

ABSTRACT. - The KEOPS cruise took place during the austral summer of 2005 on the Kerguelen Plateau. The annual bloom of the plateau is correlated with the iron supply from bottom waters as a result of internal waves generated by the tide. Fertilization allows an intense bloom of diatoms that use the stock of available silicic acid; silicon becomes limiting at the end of the productive period. Surprisingly, the intensity of nitrogen regeneration maintains the use of the nitrate stock at a very low level and diatoms grow using ammonium regenerated by heterotrophs. The phytoplankton assemblages that develop in the core of the bloom are very different from those encountered in the HNLC (high nutrient, low chlorophyll) area. Diatom biodiversity is affected by the fertilization process. The development of the bloom leads to a decrease in concentrations of dissolved inorganic carbon (DIC) and an increased vertical export of carbon. The results of KEOPS highlight the complex behavior of natural systems and the major differences with results obtained by artificial mesoscale fertilization experiments.

RÉSUMÉ. - Augmentations de la production primaire et de l'exportation verticale de carbone sur le plateau de Kerguelen en relation avec la fertilisation naturelle en fer dans un environnement HNLC (high nutrient, low chlorophyll).

La campagne KEOPS s'est déroulée durant l'été austral 2005 sur le plateau de Kerguelen. Le bloom annuel du plateau est corrélé à un apport en fer à partir des eaux de fond sous l'effet d'ondes internes générées par la marée. La fertilisation permet une floraison intense de diatomées qui utilisent le stock d'acide silicique disponible ; le silicium devient ainsi limitant en fin de période productive. De manière surprenante, l'intensité de la régénération de l'azote a pour conséquence de maintenir l'utilisation du stock de nitrate à un niveau très faible et les diatomées se développent alors en utilisant l'ammonium régénéré par les hétérotrophes. Les assemblages phytoplanctoniques qui se développent au centre du bloom diffèrent fortement de ceux rencontrés dans la zone HNLC. La biodiversité des diatomées est donc affectée par le processus de fertilisation. Le développement du bloom se traduit par une diminution des concentrations en carbone inorganique dissous (DIC) et une exportation verticale de carbone exacerbée. Les résultats de KEOPS mettent en évidence le comportement complexe des systèmes naturels et les grandes différences avec les expériences de fertilisation artificielle à méso-échelle.

Key words. - Iron limitation - Natural fertilization - Diatom communities - Bloom - HNLC ecosystem.

The Southern Ocean is home to the largest HNLC (high nutrient low chlorophyll) region of the World Ocean. Waters of the Permanently Open Ocean Zone (POOZ) and those of the Polar Frontal Zone (PFZ) are among the richest in nutrients in the World Ocean, but have extremely low biomass, most often formed by the small fraction of picophytoplankton (Jochem *et al*., 1995). Studies conducted since the historical period to the present day have shown the important role played by the availability of iron in limiting primary production in these waters. Within this oceanic desert, the existence of oases enriched by phytoplankton was rapidly identified by the pioneering work of Hart (1934) who coined the expression 'land effect' to suggest the role of iron inputs in such areas. The issue of iron took a controversial turn with the 'iron hypothesis' of Martin (1990), deduced from the negative correlation between dust concentrations and atmospheric CO_2 concentrations in the Vostok ice core spanning the last 160 000 years. Shortly after, the first microcosm studies in ultra-clean conditions brought the first demonstration of the role of iron in limiting the use of nitrate by Antarctic phytoplankton (De Baar *et al*., 1990; Martin and Fitzwater, 1990). Yet it was not until the first mesoscale artificial enrichment experiments that it was unambiguously demonstrated that the addition of iron in the POOZ waters resulted in an increase in primary production. This demonstration is credited to the Southern Ocean Iron Release Experiment (SOIREE), the first *in situ* iron fertilisation experiment performed in the polar waters of the Southern Ocean (Boyd *et al*., 2000). Several experiments followed (see review by Boyd *et al*., 2007) but were unsuccessful in determining if artificial fertiliza-

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(1) Laboratoire d'océanographie physique et biogéochimique, UMR 6535, CNRS/IRD/ Université de la Méditerranée, Marseille, France.
(2) Laboratoire d'océanographie microbiologique, UMR 7621, CNRS/Université Pierre & Marie Curie, Banyuls-sur-Mer, France. [Stephane.blain@obs-banyuls.fr]
(3) Institute of Antarctic and Southern Ocean Studies, University of Tasmania, Hobart, Australia. [Tom.trull@utas.edu.au]
* Corresponding author [bernard.queguiner@univmed.fr]

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tion resulted in the increase of vertical carbon export to deep waters or was a simple transient phenomenon returning CO_2 to the atmosphere over a short time period.

In this context, the Kerguelen Ocean and Plateau compared Study (KEOPS) Program has developed a new concept: a natural laboratory for studying the response of the marine environment to a natural disturbance, consisting of an ecosystem naturally fertilized with iron in an otherwise HNLC environment. Details of the KEOPS program are reported elsewhere by Blain *et al*. (2007, 2008). Here we focus on four questions addressed during KEOPS: 1) Is iron availability a driver of phytoplankton bloom Southeast of Kerguelen Islands? 2) What are the consequences on major nutrient utilization? 3) What is the ecosystem structure in and out of the bloom area? And, finally 4) what are the effects of the bloom on pCO_2 and carbon export to depth?

AREA DESCRIPTION AND OVERALL STRATEGY OF KEOPS

The largest phytoplankton bloom inside an HNLC area of the Southern Ocean is observed around Kerguelen Islands and the adjacent plateau to its southeast, south of the Polar Front (45 000 km^2). The scientific objectives of KEOPS were to identify a study site and demonstrate the process of natural iron fertilization in the Southern Ocean, study the impact of natural fertilization on the first trophic levels of the ecosystem, and evaluate the impact of natural fertilization on biogeochemical cycles particularly that of carbon. The scientific strategy of KEOPS was based on the comparative study of a fertilized site *vs* an HNLC type reference site. Ocean colour remote sensing was used to position the two contrasting stations and adjust transect stations before and during the cruise. We identified and followed a station in the core of the bloom area (A3) and another one in a tongue of well-defined HNLC water (C11) (Fig. 1). In summary, the strategy of the study consisted of describing the spatial extent of the bloom and the temporal evolution at the two control stations using vertical profiles of measurements of physical parameters, i.e., conductivity, temperature, depth (CTD) and sampling of biogeochemical parameters (Rosette sampler, net tows, as well as ultra-clean bottles for iron). Biogeochemical cycles of carbon, nitrogen and silicon, and the bacterial, phytoplankton, and zooplankton community structures have been the subject of special attention (for details, see Blain *et al*., 2008).

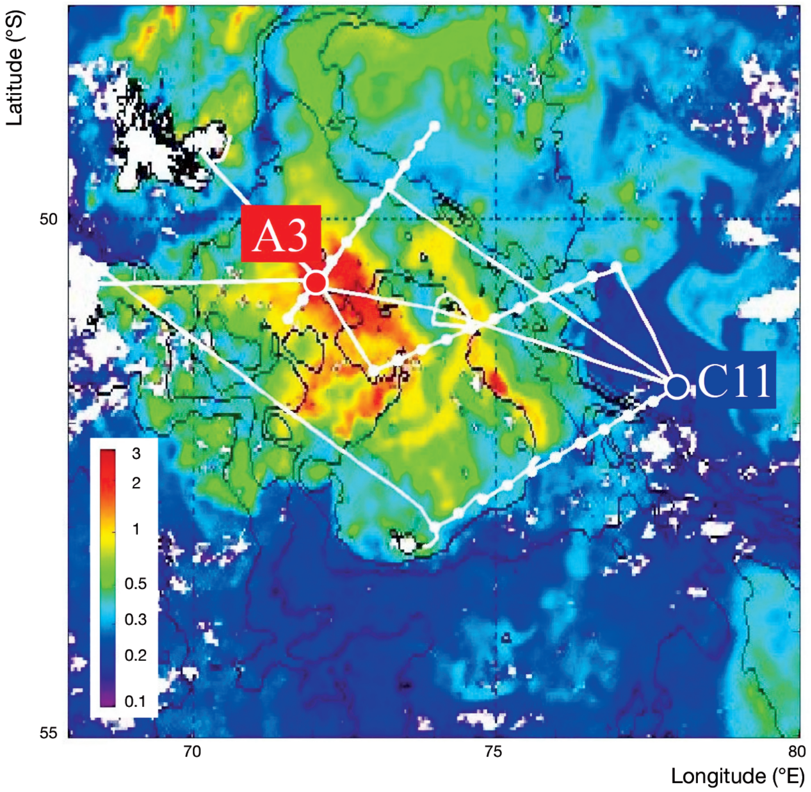

Figure 1. - Map of the study area and MERIS and MODIS merged chlorophyll *a* concentrations (ACRI Processing, Coastwatch product) on 21 January 2005.

RESULTS

The process of natural iron fertilization in the southeastern Kerguelen bloom

The validation of the concept of a natural laboratory required the demonstration of fertilization of the Kerguelen Plateau waters with iron. The vertical distribution of dissolved iron clearly demonstrated that Kerguelen Plateau deep waters were enriched with iron (0.35 nM on average at 500 m depth), but due to bloom development, surface waters were almost as depleted as in the HNLC area (mean value over the study area on and off the plateau: 0.090 ± 0.034 nM; Blain *et al*., 2007). It was then necessary to understand the mechanism by which the surface layer remains rich enough in iron to allow the phytoplankton to maintain its biomass for nearly four months (the bloom period corresponds to the period from November to February). A time series of CTD profiles showed the existence of internal waves whose activity substantially increases the vertical diffusivity coefficient (K_z) and enhances the vertical transport of solutes (including iron) from below towards the surface layer (Park *et al*., 2008). This, combined with a greater winter stock of dissolved iron

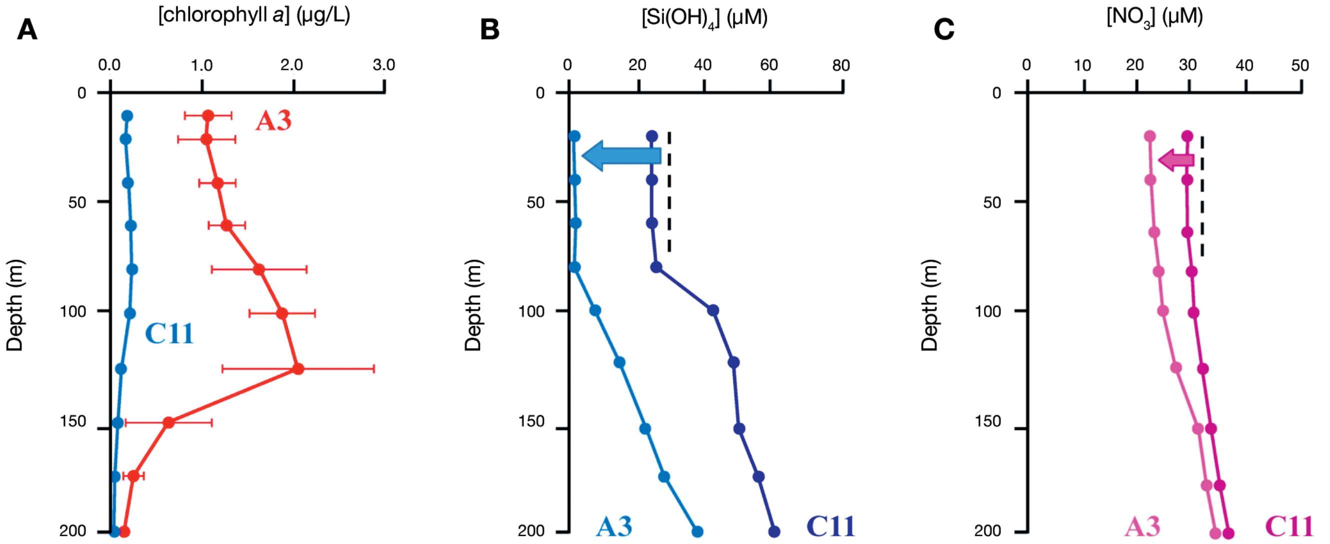

Figure 2. - Comparison between the two reference stations of KEOPS. **A**: Average concentrations of chlorophyll *a*; **B**: Average concentrations of orthosilicic acid; **C**: Average concentrations of nitrate, in the surface layer. The arrows indicate the progression from winter values of the mixed layer (dashed lines) and observed values at the end of the productive period (data from Mosseri *et al*., 2008; Jouandet, 2008; Jabaud-Jan *et al*., 2004).

and a steeper vertical gradient over the plateau as compared to the offshore HNLC system, was able to maintain the phytoplankton population in somewhat iron-replete conditions in the core of the bloom. Consequently, the chlorophyll *a* (Chl *a*) biomass (Fig. 2A) was much higher above the plateau (1.1-2.1 mg L^{-1} between 0 and 125 m at A3) as compared to the off-plateau area (0.1-0.2 mg L^{-1} between 0 and 125 m at C11) (Mosseri *et al*., 2008). This contrast was also highlighted in terms of primary production. The integrated daily primary production was ~4x higher in the Fe-enriched area (82.37 ± 4.8 mmol m^{-2} d^{-1}) as compared to the HNLC waters (22.37 ± 4.5 mmol m^{-2} d^{-1}). Mosseri *et al*. (2008) also reported that most of the production of the Fe-enriched area was due to the large phytoplankton (~80% in the > 10 μm size class at A3 *vs* ~35% at C11).

Nitrate and Silicic acid utilization in relation to iron availability

Iron limitation typically results in restricting the use of NO_3 (nitrate) versus H_4SiO_4 (silicic acid) which leads to the occurrence of strongly silicified diatoms; HNLC-type waters enriched with iron are characterized instead by diatoms that use NO_3 and H_4SiO_4 in a stoichiometric ratio close to 1 (Hutchins and Bruland, 1998; Takeda, 1998). Although they have not been directly measured, Kerguelen Plateau winter concentrations are considered to be close to 27 μM H_4SiO_4 (Jouandet, 2008) and 31.5 to 33 μM NO_3 (Jabaud-Jan *et al*., 2004). Given the uncertainties of winter concentrations one can reasonably estimate that the use of nutrients by diatoms, resulting from cessation from iron limitation, eventually should lead to a concomitant depletion of NO_3 and H_4SiO_4 in the fertilized waters. Surprisingly, this was exactly contrary to observations during the KEOPS experiment (Fig. 2B, 2C). At C11, low Chl *a* concentrations paralleled high levels of surface H_4SiO_4, NO_3, and phosphate (PO_4) concentrations, respectively averaging 25.1, 29.4 and 2.1 μM in the upper 80 m, typical of HNLC conditions. At A3, the stock of $H_4SiO_4$was quite depleted (average: 1.8 μM in the upper 80 m) but NO_3 and PO_4 were still very high (average values: 23.0 and 1.7 μM, respectively, in the upper 80 m) (Mosseri *et al*., 2008). The importance of residual stocks of NO_3 and PO_4 has been interpreted as resulting from a rapid remineralization of nitrogen and probably phosphorus in the fertilized area. There are no data regarding the regeneration of phosphorus, but for nitrogen, high concentrations of ammonium (NH_4) were observed in the bloom area. Mosseri *et al*. (2008) indicated that large variations of NH_4 concentrations occurred between the repeat visits at the two reference stations and that high levels of NH_4 were found at A3 marked by a peak averaging 1.9 μM at 125 m, coinciding with the deep Chl *a* maximum. For that reason, the integrated NO_3-based production was only ~2.5 times higher in the Fe-enriched area but the integrated NH_4-based production accounted for more than 50% of the nitrogen production. Finally, Mosseri *et al*. (2008) reported higher affinities for H_4SiO_4 on the Kerguelen plateau, as compared to the HNLC region, as a result of iron availability as already mentioned by Quéguiner (2001). K_S values at A3 (5-15μM) were always higher than the ambient H_4SiO_4 concentration (~1.8 μM), indicating that diatom silicification was limited by external concentrations

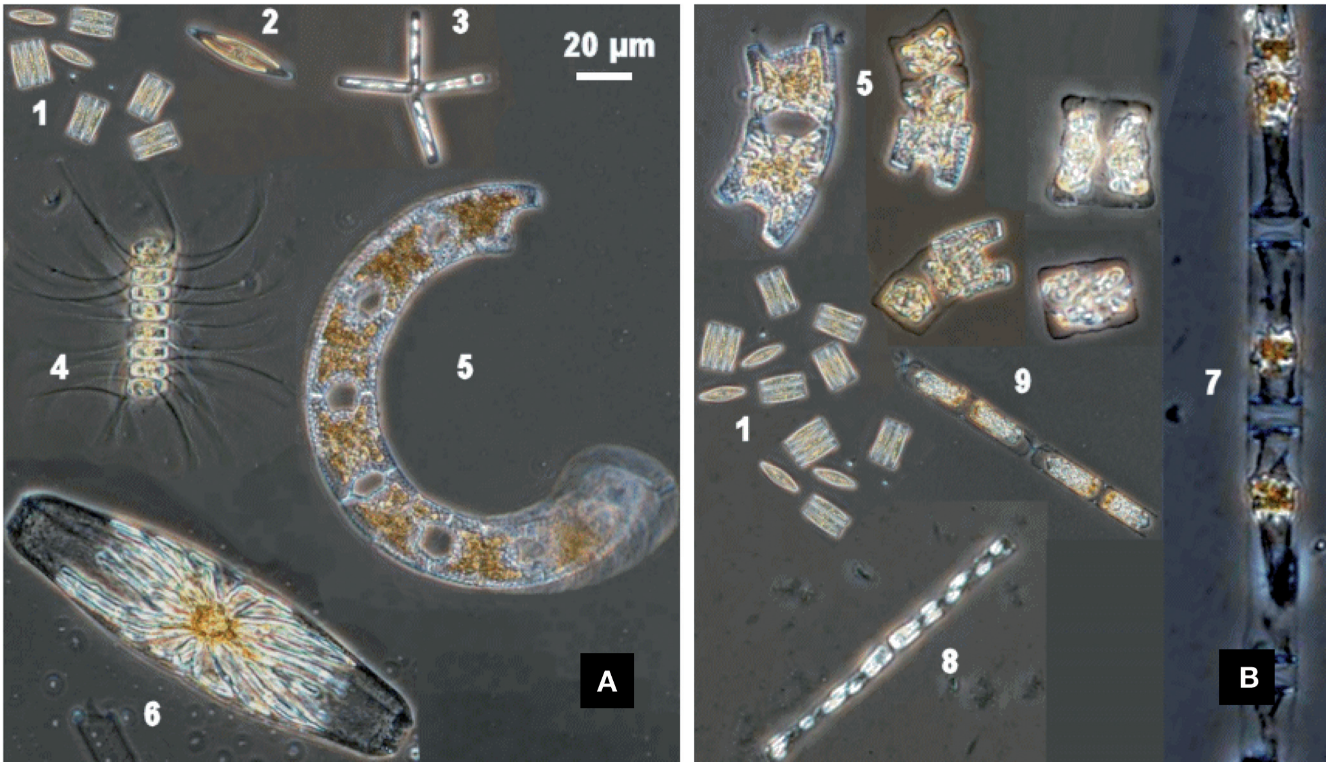

Figure 3. - Composite illustration of phytoplankton assemblages at station A3 at the beginning (**A**) and the end (**B**) of the KEOPS cruise. 1. *Fragilariopsis kerguelensis*, 2. *Navicula* sp., 3. *Thalassionema nitzschioides*, 4. *Chaetoceros debilis*, 5. *Eucampia antarctica*, 6. *Membraneis* sp., 7. *Corethron inerme*, 8. *Leptocylindrus danicus*, 9. *Guinardia cylindrus*.

in the late phase of the bloom that characterized the time window of KEOPS. This limitation of diatoms production by silicon explains the low rates of biogenic silica production that were observed at both reference stations. However the Si/C stoichiometric production ratios were much lower in the core of the bloom (0.14-0.06) at A3 as compared to the typical HNLC conditions at C11 (0.34-0.44). This indicated that phytoplankton was more heavily silicified under HNLC conditions, which is generally accepted since the work of Hutchins and Bruland (1998) and Takeda (1998).

Microphytoplankton communities

Sampling for microphytoplankton communities was done in two ways: water samples from the hydrological casts and net tows.

Successive water samples at the bloom station A3 revealed an evolution from an assemblage dominated by *Chaetoceros*, subgenus Hyalochaetae Ehrenberg 1844/ Gran 1897 to a remnant assemblage dominated by *Eucampia antarctica* (Castracane) Mangin 1914 (Armand *et al*., 2008a). The initial assemblage at A3 (Fig. 3A) contained representatives of *Chaetoceros debilis* Cleve 1894 as the main species of the Hyalochaetae group, *Fragilariopsis kerguelensis* (O'Meara) Hustedt 1952, *Navicula* sp. Bory de Saint-Vincent 1822, *Thalassionema nitzschioides* (Grunow) Mereschkowsky 1902, *E. antarctica*, and *Membraneis* sp. Paddock 1988. In the final assemblage at A3 (Fig. 3B) *E. antarctica* was often present as resting stages and was accompanied by *F. kerguelensis*, *Corethron inerme* Karsten 1905, *Leptocylindrus danicus* Cleve 1889, and *Guinardia cylindrus* (Cleve) Hasle 1996 (Armand *et al*., 2008a). The temporal evolution of the diatom assemblage at A3 probably reflected the intensification of limitation of H_4SiO_4 at the end of the bloom. In contrast with the situation on the plateau and the importance of large centric diatoms, the phytoplankton assemblages observed during the successive visits to the HNLC reference station always showed dominance by the small pennate diatoms *F. pseudonana* (Hasle) Hasle 1993 and *F. kerguelensis* (Armand *et al*., 2008 a).

During KEOPS, at the center of the bloom, the comparison between water samples and net tows indicated the presence of two different kinds of diatom populations. By contrast to the assemblages described above, net tows were dominated by large colonies of the heavily silicified pennate diatoms *F. kerguelensis* accompanied by the giant *Thalassiothrix antarctica* A. Schimper ex-G.Karsten, 1905 (Armand *et al*., 2008a). It seemed that we were dealing with two diatom communities occupying two distinct niches in the epipelagic domain: numerous centric diatoms distributed homogeneously in the mixed layer and pennate diatoms

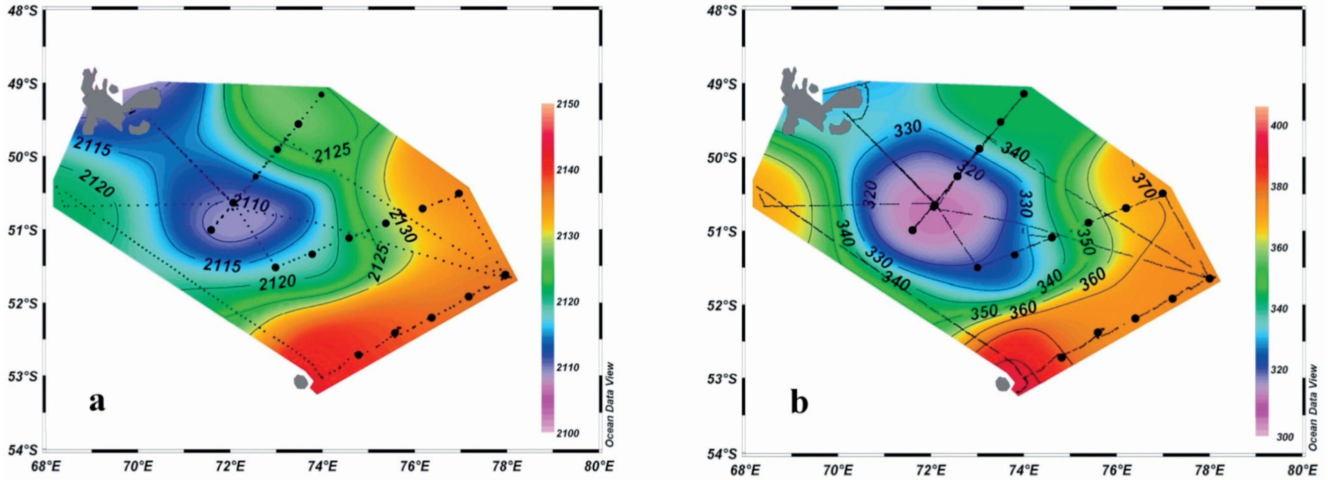

Figure 4. - Distributions of dissolved inorganic carbon (DIC, µmol kg^{-1}) (a) and oceanic fugacity of CO_2 ($fCO_{2\ \mathrm{ocean}}$, µatm) (b) in surface waters (5 m depth) based on continuous measurements made on board N.O. *Marion Dufresne 2* during KEOPS.

heterogeneously distributed, constituting perhaps discrete micro-layers at the base of the mixed layer, or a 'shade flora' *sensu* Sournia (1982), and developing a survival strategy based on resistance to herbivory as suggested by Smetacek *et al*. (2004). Empty frustules of *F. kerguelensis* represent 31% of the remains of diatoms in the surface sediment of the Kerguelen Plateau, and 57% in the HNLC area (Armand *et al*., 2008b). It is therefore possible that the two types of assemblages represent two different pathways of transfer of biogenic matter fueling either the pelagic food webs or the sedimentary opal flux. Either way, these results suggest that the use of diatom thanatocoenoses to determine past productivity events is not straightforward as pointed out by Armand *et al*. (2008b).

Iron enrichment and the biological pump

Gas exchanges at the ocean-atmosphere interface are proportional to the difference of fugacities (fCO_2) between water and air. During the KEOPS cruise, average atmospheric fugacity ($fCO_{2\ \mathrm{air}}$) was estimated at 372.3 ± 0.5 μatm. The distributions of dissolved inorganic carbon (DIC) concentrations and oceanic fugacities ($fCO_{2\ \mathrm{ocean}}$) are shown in figure 4. Results of Jouandet *et al*. (2008) indicated that the bloom area was characterized by low DIC and $fCO_{2\ \mathrm{ocean}}$ values (2114 ± 8 µmol kg^{-1} and 311 ± 8 µatm respectively), indicating the enhancement of the biological pump in the iron-fertilized zone. There was a sharp contrast with the area outside of the bloom where average values of $fCO_{2\ \mathrm{ocean}}$ and DIC were 372 ± 6 µatm and 2 135 ± 5 µmol kg^{-1} respectively. Consequently, the waters around C11 represented the maximum CO_2 source vis-à-vis the atmosphere ($\Delta fCO_2 = +3$ µatm) while the waters around A3 represented a significant net sink of CO_2 ($\Delta fCO_2 = -71.3$ µatm). The vertical organic carbon export was estimated using the deficit of ^{234}Th activity in the water column, and the ratio of particulate organic carbon (POC) to ^{234}Th measured from sampling by *in situ* pumps. Results indicated that the POC export at the base of the surface mixed layer from the bloom over the plateau was approximately 2.5 times as large as in the HNLC waters off the plateau with values of 24.5 and 10.3 mmol C m^{-2} d^{-1} respectively (Blain *et al*., 2007; Savoye *et al*., 2008).

DISCUSSION

Natural *vs* artificial iron fertilization experiments

Since the controversial article by Martin (1990) it has been suggested that fertilizing the ocean with iron could be used in climate geoengineering to mitigate atmospheric CO_2 concentrations (Boyd, 2008). The question that arose then was to what extent iron fertilization could increase surface primary production and, overall, export carbon to deep waters, as this is the only way to get a lasting effect of CO_2 sequestration. To elucidate the role of iron in the HNLC ecosystem functioning over a dozen of mesoscale fertilization, experiments have been conducted in different parts of the World Ocean. All of these experiments have measured the effects of adding iron such as an increase in phytoplankton biomass associated to an increase of surface primary production and a drawdown, although of variable intensity, of DIC in surface waters (Boyd *et al*., 2007). The impact of artificial fertilizations on vertical export is much more difficult to assess. The results obtained during KEOPS indicate a decrease of fCO_2 within the Kerguelen bloom which is 2.5 fold higher (Jouandet *et al*., 2008), and a sequestration efficiency (mol C exported *vs* mol Fe supply) on the order of 10 times higher (Blain *et al*., 2007), than those measured during artificial iron enrichment experiments. Blain *et al*.

(2007) attribute this higher efficiency of the natural fertilization to the mode of natural iron fertilization characterized by a continuous slow supply which prevents massive iron loss characteristic of mesoscale fertilization experiments. Using polyacrylamide gels in short-term free-drifting sediment trap deployments, Ebersbach and Trull (2008) also report that the majority of the particle flux was processed through the heterotrophic food web contrasting again with the results of artificial iron-fertilization experiments. Although mesoscale experiments provided much information on the dynamics of iron in the epipelagic zone, their extrapolation to the global scale remains risky. One of the major achievements of KEOPS has been to indicate that the efficiency of the biological pump in naturally iron-fertilized systems is in fact controlled by complex interactive processes that combine circulation of water masses, vertical exchange, geochemical reactions and biological response of food webs and microbial communities.

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REFERENCES

ARMAND L.K., CORNET-BARTHAUX V., MOSSERI J. & QUÉGUINER B., 2008a. - Late summer diatom biomass and community structure on and around the naturally iron-fertilized Kerguelen Plateau in the Southern Ocean, *Deep-Sea Res. II*, 55: 653-676.

ARMAND L.K., CROSTA X., QUÉGUINER B., MOSSERI J. & GARCIA N., 2008b. - Diatoms preserved in surface sediments of the northeastern Kerguelen Plateau, *Deep-Sea Res. II*, 55: 677-692.

BLAIN S., QUÉGUINER B. & TRULL T., 2008. - The natural iron fertilization experiment KEOPS (KErguelen Ocean and Plateau compared Study): An overview. *Deep-Sea Res. II*, 55: 559-565.

BLAIN S., QUÉGUINER B., ARMAND L. *et al*. (47 authors), 2007. - Effect of natural iron fertilization on carbon sequestration in the Southern Ocean. *Nature*, 446: 1070-1075.

BOYD P.W., 2008. - Implications of large-scale iron fertilization of the oceans. *Mar. Ecol. Prog. Ser.*, 364: 213-218.

BOYD P.W., JICKELLS T., LAW C.S. *et al*. (23 authors), 2007. - Mesoscale iron enrichment experiments 1993-2005: Synthesis and future directions. *Science*, 315: 612-617.

BOYD P.W., WATSON A.J., LAW C.S. *et al*. (35 authors), 2000. - A mesoscale phytoplankton bloom in the polar Southern Ocean stimulated by iron fertilization. *Nature*, 407: 695-702.

DE BAAR H.J.W., BUMA A.G.J., NOLTING R.F., CADEE G.C., JACQUES G. & TREGUER P., 1990. - On iron limitation of the Southern Ocean: experimental observations in the Weddell and Scotia Seas. *Mar. Ecol. Prog. Ser.*, 65: 105-122.

EBERSBACH F. & TRULL T.W. 2008. - Sinking particle properties from polyacrylamide gels during the KErguelen Ocean and Plateau compared Study (KEOPS): Zooplankton control of carbon export in an area of persistent natural iron inputs in the Southern Ocean. *Limnol. Oceanogr.*, 53: 212-224.

HART T.J., 1934. - On the phytoplankton of the Southwest Atlantic and the Bellingshausen Sea 1929-1931. *'Discovery' Rep.*, 8: 1-268.

HUTCHINS D.A. & BRULAND K.W., 1998. - Iron-limited diatom growth and Si:N uptake ratios in a coastal upwelling regime. *Nature*, 393: 561-564.

JABAUD-JAN A., METZL N., BRUNET C., POISSON A. & SCHAUER B., 2004. - Interannual variability of the carbon dioxide system in the southern Indian Ocean (20°S-60°S): The impact of a warm anomaly in austral summer 1998, *Global Biogeochem. Cycles*, 18, doi:10.1029/2002GB002017.

JOCHEM F.J., MATHOT S. & QUÉGUINER B., 1995. - Size-fractionated primary production in the open Southern Ocean in austral spring. *Polar Biol.*, 15: 381-392.

JOUANDET M.-P., 2008. - Impact d'une fertilisation naturelle en fer sur le cycle du carbone océanique (Iles Kerguelen, Océan Austral). Thèse de Doctorat en Sciences de l'Environnement Marin, 131 p. Univ. de la Méditerranée, Marseille, France.

MARTIN J.H. & FITZWATER S.E., 1990. - Iron deficiency limits phytoplankton growth in Antarctic waters. *Global Biogeochem. Cycles*, 4: 5-12.

MARTIN J.H., 1990. - Glacial-interglacial CO_2 change: The iron hypothesis. *Paleoceanography*, 5: 1-13.

MOSSERI J., QUÉGUINER B., ARMAND L.K. & CORNET-BARTHAUX V., 2008. - Impact of iron on silicon utilization by diatoms in the Southern Ocean: A case study of Si/N cycle decoupling in a naturally iron-enriched area. *Deep-Sea Res. II*, 55: 801-819.

PARK Y.-H., FUDA J.-L., DURAND I. & NAVEIRA G.A.C., 2008. - Internal tides and vertical mixing over the Kerguelen Plateau. *Deep-Sea Res. II*, 55: 582-593.

QUÉGUINER B., 2001. - Biogenic silica production in the Australian sector of the Subantarctic Zone of the Southern Ocean in late summer 1998. *J. Geophys. Res.*, 106: 31,627-31,636.

SAVOYE N., TRULL T.W., JACQUET S.H.M., NAVEZ J. & DEHAIRS F., 2008. - ^{234}Th-based export fluxes during a natural iron fertilization experiment in the Southern Ocean (KEOPS). *Deep-Sea Res. II*, 55: 841-855, 2008.

SMETACEK V., ASSMY P. & HENJES J., 2004. - The role of grazing in structuring Southern Ocean pelagic ecosystems and biogeochemical cycles. *Antarct. Sci.*, 16: 541-558.

SOURNIA A., 1982. - Is there a shade flora in the marine plankton? *J. Plankt. Res.*, 4: 391-400.

TAKEDA S., 1998. - Influence of iron availability on nutrient consumption ratio of diatoms in oceanic waters. *Nature*, 393; 774-777.